

INTERACTIONS BETWEEN INVERTEBRATES AND MICROORGANISMS: NOISE OR NECESSITY FOR SOIL PROCESSES?

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INTRODUCTION

The operation of soil microbial processes at a gross level is well understood and this knowledge continues to be refined and applied in forestry and agricultural management practices. There has, however, been little explicit recognition of the complexity of the processes regulating nutrient fluxes between litter, soil and plant roots (Frissel & van Veen, 1982). Mechanisms of decomposition and nutrient transformation in soils are usually interpreted in terms of a simple sequence of steps mediated by microorganisms and the roles of invertebrates in these processes are rarely invoked (Anderson & Ineson, 1984). In fact, this is a manifestation of a general dichotomy in soil biology (and perhaps in soil biochemistry) between descriptive and process-orientated research. Swift (1984) contends that studies on the role of microorganisms in decomposition processes fall into two main schools. In one approach the decomposer organisms are broadly defined as 'driving variables' promoting the processes of carbon and nutrient mineralization with little explicit recognition of the structure of the microbial community. This contrasts with the second school which has been concerned with the diversity of decomposer species, and their distribution, abundance and activities. Similar trends are evident in soil zoology (Satchell, 1974; Usher, Booth & Sparks, 1982).

The net result of these two approaches is that we have considerable difficulty integrating information relating to specific organisms into the understanding of soil processes operating on less defined spatial and temporal scales. The fundamental question is whether there are significant functional attributes of these diverse systems, or do the complex interactions of the component species in the community represent 'background noise' which is filtered out through the net contribution of microsite processes to ecosystem-level fluxes of carbon or nutrients?

There is very extensive literature on these interactions which has been reviewed comprehensively elsewhere (Anderson, Coleman & Cole, 1981; Satchell, 1983; Anderson, Rayner & Walton, 1984; Seastedt, 1984; Fitter *et al.*, 1985). Emphasis in this paper is placed on their functional importance for decomposition and nutrient cycling through direct and indirect effects on soil processes. The relative contributions of these effects in a system is determined by spatial and temporal scales on which the organisms interact.

SPATIO-TEMPORAL SCALES OF INTERACTIONS

In very general terms animal-microbial interactions may be considered to operate on micro-, meso- and macro-scales in space and time which are a function of the relative body sizes (Fig. 1) of the

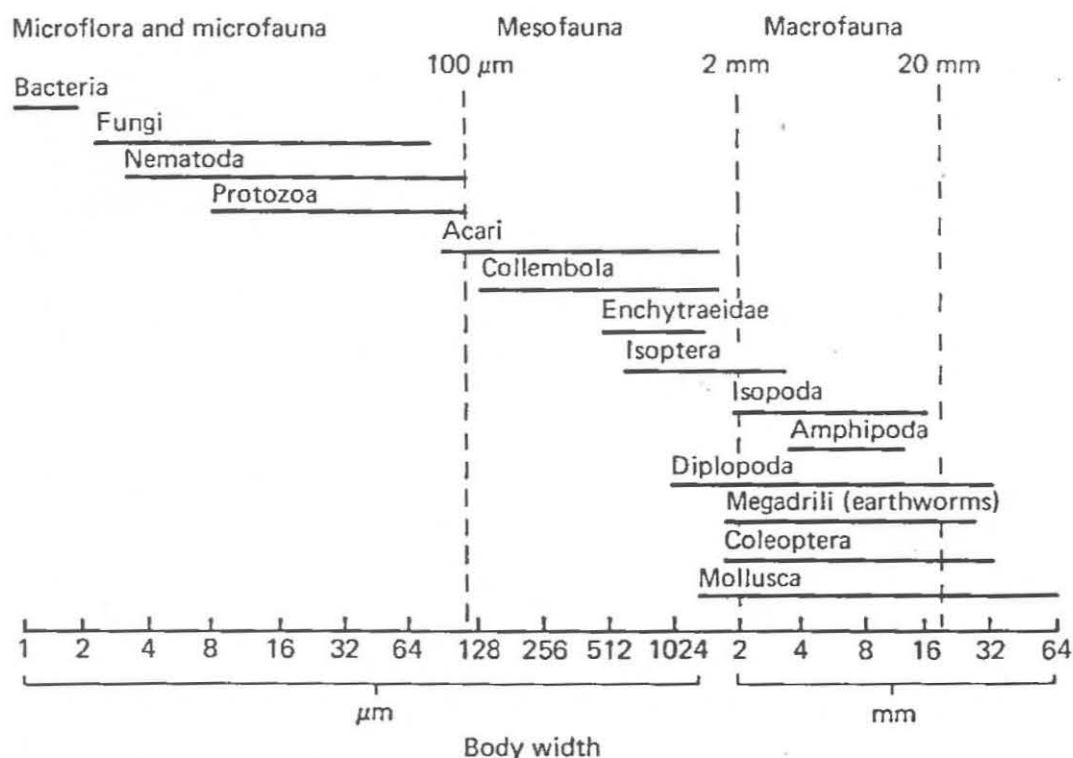


Fig. 1. Functional classification of soil organisms by body width. (After Swift, Heal & Anderson, 1979.)

organisms. The feeding activities of nematodes and protozoans (microfauna) operate within the water-filled pores and surface films of the soil matrix at similar scales to bacteria and fungal hyphae. These microfauna also have comparable generation times, of hours or days, to bacteria and fungi, and are hence able to respond rapidly to temporal changes in microbial populations subject to the constraints

placed on their feeding activities by soil pore-size distributions. Collembolans and mites (mesofauna) generally live on litter surfaces and in air-filled macropores in soil. Many species are mycophagous but the proportion of higher plant material ingested increases as a positive function of body size (Anderson, 1975), suggesting that the smaller species are able to feed more selectively on fungi. The generation times of soil mites and collembolans are of the order of weeks or months so that their populations are likely to respond to changes in the quality and quantity of fungal biomass over comparable periods of time. Enchytraeids, fly larvae and some mites have more burrowing habits and in acid woodland soils their faeces may constitute a large and definitive component of the humus fabric (Kubiena, 1953; Rusek, 1985).

The feeding and burrowing activities of the macrofauna transcend most of the microhabitat constraints on the interactions between microorganisms and the smaller groups of soil invertebrates in litter and soil. Hence macrofaunal effects on bacteria and fungi depend upon the frequency of these perturbations to microbial habitats and the phenological responses of the microorganisms.

The indirect physical effects of animals on microbial populations and activities thus increase with increasing body size, but as the body size of invertebrates increases the weight-specific metabolic rates generally decrease within a trophic group. Hence the microfauna, with a small biomass but high densities of individuals and rapid turnover, will have a larger direct metabolic contribution to carbon and nitrogen fluxes through consumption of microorganisms than the same biomass of macrofauna (Petersen & Luxton, 1982).

The direct and indirect effects of invertebrates on microbial populations and nutrient mineralization can be viewed therefore as reciprocal processes with their relative contributions to soil processes determined by the structure of the soil organism community.

DIRECT CONTRIBUTIONS OF INVERTEBRATES TO SOIL PROCESSES

Most of the studies on the nutrient dynamics of bacteriophagy and mycophagy by nematodes and protozoans have been carried out in microcosms set up as analogues of microsite conditions in bulk soils or the rhizosphere. These studies have shown that the microfauna can regulate bacterial and fungal growth dynamics and nutrient

uptake by plants. Seedlings of the grass *Bouteloua gracilis* growing with either bacteriophagous protozoans (Elliott, Coleman & Cole, 1979) or mycophagous nematodes (Ingham *et al.*, 1985) showed increased growth and foliar nitrogen concentrations in comparison with controls without animals. Similarly, Clarholm (1985a) has grown wheat plants with and without protozoans in autoclaved arable soil which had been reinoculated with a natural bacterial flora. After 6 weeks the plants grown in soil with protozoans had a 60% larger mass and a higher shoot/root biomass ratio than controls with bacteria only. The mechanism invoked for this effect is the stimulation of carbon-limited bacteria by root exudates as the root invades soil microsites. A third of the nitrogen immobilized by the growth of the bacteria is then released as excretory ammonium ions by protozoans feeding in the rhizosphere. The quantitative importance of these rhizosphere processes has not been demonstrated under field conditions but it is unlikely that they contribute significantly to the mineral nitrogen available to arable crops. Rooting densities greater than 10 cm^{-2} have rarely been found in spaced crops and only sparsely distributed roots ($<1\text{ cm}^{-2}$) are needed to exploit nitrate reserves fully in the soil solution (Nye & Tinker, 1977). The difficulty of extrapolating these microsite mechanisms to the field does not negate the potential importance of faunal impacts on microbial processes of nutrient immobilization and release in bulk soil. Reciprocal seasonal trends in protozoan and microbial biomass phosphorus have been demonstrated in a wheat-fallow soil (Fig. 2) and the predator-prey basis of this relationship is supported by calculations for a grassland soil that protozoans (mainly amoebae) can consume four times the mean bacterial biomass per year (Elliott & Coleman, 1977).

More precise estimates of faunal contributions to ecosystem nutrient fluxes are derived from budgets on the feeding, excretion and population dynamics of the component species or functional groups in the community. Some of the most comprehensive studies of this kind have been carried out within the Swedish Ecology of Arable Lands Programme (Rosswall & Paustian, 1984). Detailed nitrogen budgets have been drawn up for four cropping systems: a lucerne ley without fertilizer; a grass ley receiving $200\text{ kg N ha}^{-1}\text{ a}^{-1}$; barley receiving $120\text{ kg N ha}^{-1}\text{ a}^{-1}$; and barley without fertilizer nitrogen. Results are summarized in Table 1. It was concluded that only the protozoan and nematode faunas excreted significant amounts of mineral nitrogen which was highest in the fertilized grass ley

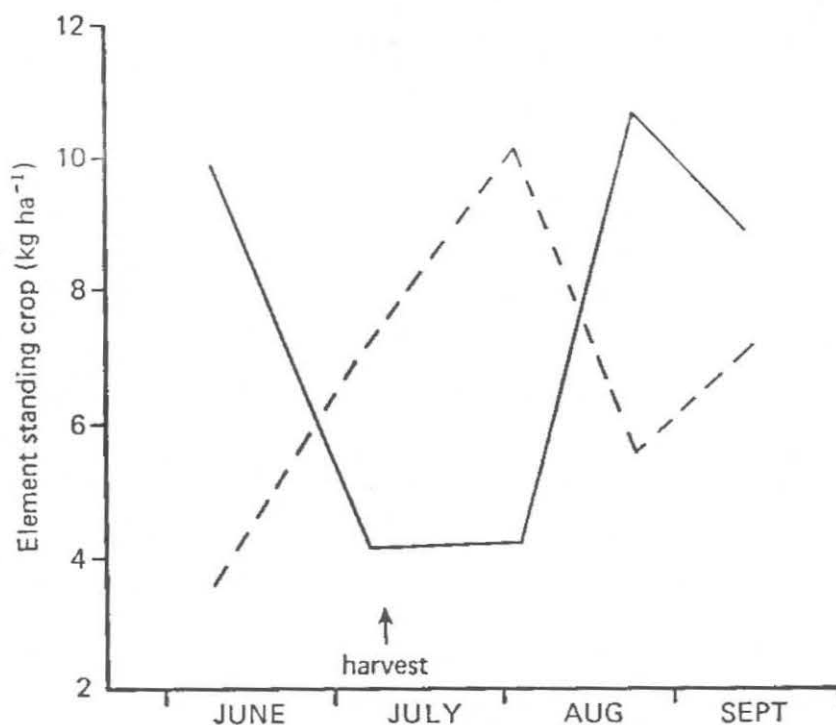


Fig. 2. Dynamics of microbial biomass phosphorus (---) and protozoan carbon (—) in a no-till wheat field (Colorado). Biomass element pools were determined by chloroform fumigation. The values for protozoan carbon have been multiplied by 5. (After Ingham *et al.*, 1985.)

(19% of $25.7 \text{ g m}^{-2} \text{ a}^{-1}$, i.e. about $50 \text{ kg ha}^{-1} \text{ a}^{-1}$) and lowest in the barley plots ($38\text{--}40 \text{ kg ha}^{-1} \text{ a}^{-1}$). However, the percentage of total mineralization attributed to faunal consumption of bacteria and fungi was about a third of the total flux in the barley plots compared with a fifth in the leys. A similar contribution of fauna to total nitrogen mineralization was calculated for a Swedish pine forest by Persson (1983). Here the soil fauna biomass was only 1.7 g m^{-2} (in comparison with 120 g m^{-2} fungi and 39 g m^{-2} bacteria) and represented only 4% of heterotroph metabolism. However, the animals consumed 30–60% of microbial production and hence contributed 10–49% of total nitrogen mineralization in the forest soil ($28 \text{ kg ha}^{-1} \text{ a}^{-1}$) of which nearly 70% was excretion by nematodes and protozoans.

Earthworm populations were small in both of these Swedish study areas; even in the lucerne ley the mean earthworm biomass was only $50 \text{ kg dry wt m}^{-2}$ (Lofs-Holmin & Bostrom in Clarholm, 1985b). Estimates of the mean earthworm biomass (dry weight) for temperate regions range from about 50 kg ha^{-1} in boreal forests to about 450 kg ha^{-1} in the most densely populated New Zealand pastures. Lee (1983) has calculated from these figures (assuming a production: biomass ratio of 2–5) that the turnover of nitrogen through these

Table 1. *Nitrogen mineralization and total soil organic matter nitrogen balance for four arable cropping systems in Sweden (from Rosswall & Paustian, 1984)*

Cropping system	Fertilizer treatment (kg N ha ⁻¹ a ⁻¹)	Estimated net mineralization (g m ⁻² a ⁻¹)	Relative mineralization (% of soil N)	Mineralization via fauna (% of net mineralization)	Total soil N balance (g N m ⁻² a ⁻¹)
Lucerne ley	0	21.1	2.8	20	-5.3
Meadow ley	200	25.7	3.4	19	-8.2
Barley	0	10.5	1.4	36	-8.7
Barley	120	12.8	1.8	31	-7.4

populations amounts to $10\text{--}225\text{ kg N ha}^{-1}\text{ a}^{-1}$ with excretion contributing a further $18\text{--}50\text{ kg N ha}^{-1}$. The assimilation efficiency of earthworms is low and so these populations are maintained by large throughputs of soil and litter material. With moderate or high populations of earthworms most of the plant litter is consumed each year in temperate regions and cast production ranges from $10\text{--}500\text{ tonnes ha}^{-1}\text{ a}^{-1}$. Most estimates for pastures and grasslands are about $40\text{--}50\text{ tonnes ha}^{-1}\text{ a}^{-1}$, representing a $3\text{--}4\text{ mm}$ annual increment on the soil surface (Lee, 1983). Considerable casting occurs below ground and Graff (1971) has estimated that up to 25% of the total A_h horizon in a temperate pasture could be turned over each year. The effects of this massive disturbance to soil structure through burrowing, litter consumption and gut passage are manifested in indirect effects on the microbial community.

INDIRECT EFFECTS OF INVERTEBRATES ON MICROBIAL POPULATIONS AND PROCESSES

Invertebrates have indirect effects on the structure and activities of bacteria and fungal communities through inoculum dispersal, grazing, litter comminution, gut passage and aggregate formation. Interactions at higher trophic levels also have indirect effects on microbial communities. The functional importance of these interactions for decomposition processes and plant nutrient uptake has not generally been demonstrated under field conditions and most will only be considered briefly.

Dispersal of fungal propagules

Fungal spores on invertebrate integuments are often those of common saprophytic fungi (*Mortierella*, *Cladosporium*, *Penicillium*, *Aspergillus*, etc.) found in the soil and litter horizons from which the animals were extracted. Visser (1985) reported a total of 120 taxa of fungi isolated from guts and whole-body squashes of one species of woodland collembolan (*Onychiurus subtenuis*) with higher mean numbers of propagules from animals extracted from the litter layers (2.5–5.5) than from the humus layers (2.5–3.1). There is, however, no conclusive evidence that spore carriage by microarthropods affects the composition or functioning of microbial communities colonizing resources, as judged from the exclusion experiments of Gourbière (1986), though the cortical invasion of rotten wood by

Table 2. Colonization of *Pinus radiata* roots by the ectotrophic mycorrhizal fungus *Rhizopogon luteolus* in the presence of different numbers of soil amoebae (from Chakraborty, Theodorou & Bowen, 1985)

Treatment	No. of <i>Saccamoeba</i> g ⁻¹ soil	Root length (mm)	Length of root colonized by <i>Rhizopogon</i> (mm)
<i>R. luteolus</i>	—	89	23.6
<i>R. luteolus</i> + <i>Saccamoeba</i>	846	100	5.8
<i>R. luteolus</i> + <i>Saccamoeba</i>	423	98	8.0
<i>R. luteolus</i> + <i>Saccamoeba</i>	85	102	11.3
<i>R. luteolus</i> + <i>Saccamoeba</i>	42	103	12.9

basidiomycetes may be facilitated by invertebrates (Swift & Boddy, 1984).

Grazing and Predation

A large number of studies have demonstrated important grazing effects in litter, soil and in the rhizosphere under laboratory conditions but as yet most of these phenomena have not been quantified in the field.

Laboratory and field studies

Mycophagous amoebae in pot experiments may reduce the colonization of *Pinus radiata* roots by the ectotrophic fungus *Rhizopogon luteus* (Table 2), while mycophagous nematodes can prevent the establishment of *Suillus granulatus* on *Pinus resinosa* (Sutherland & Fortin, 1968); no effects on seedling growth were demonstrated in these studies. Wiggins & Curl (1979) suggested that collembolans grazing in the rhizosphere may reduce the invasion of roots by pathogens and symbionts but Warnock, Fitter & Usher (1982) found no effects on the growth of leeks when the mycorrhizal fungus *Glomus fasciculatum* was grazed by *Folsomia candida*. Selective feeding on different species of fungi, particularly basidiomycetes, by collembolans can affect the saprophytic colonizing ability of fungi invading leaf litter (Parkinson, Visser & Whittaker, 1979) and hence the rate of litter decomposition (Newell, 1984a). However, Andrén & Schnürer (1985) found no effects of grazing on microbial respiration,

biomass or mass loss from decomposing straw but suggested that the species of collembolan used in their experiments was not predominantly mycophagous.

Field studies using litter bags have shown both increased nutrient immobilization and release in the presence of microarthropods (Seastedt, 1984). Parker *et al.* (1984) showed that nitrogen immobilization around root litter treated with pesticides in a desert soil was about twice that of untreated soil over a 3 month period and was associated with an increase in fungal biomass. It has also been suggested that tydaeid mites may indirectly regulate the decomposition of buried leaf litter by consuming bacteriophagous nematodes (Whitford *et al.*, 1982). When these mites were eliminated by pesticide treatment, the nematode populations increased dramatically, thus reducing the bacteria and yeast populations and significantly reducing the initial rates of litter decomposition. A different approach was used by Verhoef & de Goede (1985) who established cages with and without populations of litter-living, entomobryid collembolans in a pine-forest soil. After 3 months the nitrogen concentration in the defaunated litter was more than twice that of normal litter. Selective grazing by the most abundant mycophagous collembolan species, *Onychiurus latus*, in a Sitka spruce forest also appeared to determine the distribution and abundance of two litter-decomposing basidiomycetes (Newell, 1984b). *Marasmius androsaceus*, the preferred food and faster litter-decomposing species, was restricted to the surface litter layers where collembolans were scarce. In contrast, *Mycena galopus*, which was less palatable, was associated with the underlying fermentation layers where collembolans were abundant.

Variables affecting invertebrate-microbial interactions

Estimates of the percentage of fungal biomass consumed per annum by microarthropods range from 2% for cryptostigmatid mites (Mitchell & Parkinson, 1976) to 86% for the entire mycophagous invertebrate community (McBrayer, Reichle & Witkamp, 1974). Soil habitat structure and the quality of the resources exploited by the fungus appear to be important variables underpinning these trophic dynamics, though both are poorly quantified under field conditions.

Haarløv (1960) estimated that the habitat area occupied by microarthropods in a pine-forest soil was 1/170 to 1/5000 of the total

macropore surfaces, so despite the fact that hyphal lengths in pine forest-floor materials range from 10^3 to 10^5 mg^{-1} (Hunt & Fogel, 1983), only a small proportion of the active mycelium is likely to be exposed to grazing by animals. The sensitivity of the fungus to grazing, and the population responses of the invertebrates, appear to depend on the extent to which this feeding depletes the nutrient capital of the fungus.

Laboratory studies carried out under simplified and defined artificial culture conditions are surprisingly variable. Invertebrates may feed selectively or non-selectively on species of fungi and bacteria with stimulatory, neutral or inhibitory effects on microbial growth, metabolism and species interactions (Ingham *et al.*, 1985; Visser, 1985). The responses of bacteria and fungal species to culture conditions, particularly nutrient concentrations in the media, appear to be important determinants of the variable and often contradictory results.

Park (1976) found that only 8 out of 43 fungal isolates exhibited the expected pattern in which the growth and activity of cellulose-decomposing fungi is inversely proportional to the nitrogen concentration of the media. The remaining isolates showed a range of negative, neutral and non-linear responses in culture. These optimum or sub-optimum conditions affect the physical and biochemical characteristics of the fungus and hence its palatability and nutritional value to soil invertebrates. Leonard (1984) has shown that inter- and intra-specific selection of fungi by collembolans can be changed by the growth medium (soil-, leaf- or malt-extract agar), solid or liquid culture conditions, the age of the culture and the nitrogen concentration of the media. Nutrient concentrations also determine whether grazing by collembolans stimulates or inhibits fungal respiration (Hanlon, 1981) and the growth and fecundity of animals feeding on the fungus (Booth & Anderson, 1979). The interactions of these variables often result in non-linear responses in which fungal growth and activity are stimulated at low grazing intensity but are inhibited above a threshold level (Hanlon & Anderson, 1979). A similar situation has been demonstrated in mixed cultures of protozoans and/or nematodes with bacteria or fungi (Ingham *et al.*, 1985).

The implication of these responses is that while it may be possible to model these grazing effects in the laboratory, their prediction in the field requires quantification of microsite nutrient regimes and the availability of microbial tissues to invertebrates. Such data are currently unavailable.

Effects of gut transit

Several studies of earthworm gut bacteria suggest that the groups of organisms present are the same as those in the soil where the animals are living (Satchell, 1983). On the other hand, 73% of 473 bacterial strains isolated from the gut of the oligochaete *Eisenia lucens* by Marialigeti (1979) belonged to the genus *Vibrio* (including pathogenic strains of *V. cholerae*, *V. parahaemolyticus* and *V. alginolyticus*).

Discriminant analysis of isolates from the food, gut contents and faeces of a millipede (*Glomeris marginata*) and a woodlouse (*Oniscus asellus*) revealed that, although there was some overlap, the bacterial floras of the food litter and the guts were distinct (Ineson & Anderson, 1985). The most abundant isolated from the gut of both animals was *Klebsiella pneumoniae*, supporting the results of a number of similar studies on soil invertebrates, which might account for the occurrence of this coliform in sawdust, logs and other woody habitats (Ineson & Anderson, 1985). Griffiths & Woods (1985) found *Enterobacter agglomerans* was the most frequent organism isolated from the guts of *Oniscus asellus*. In other studies, *K. pneumoniae* and *E. agglomerans* were among the most abundant free-living nitrogen-fixing bacteria found in an oak woodland soil (Jones & Bangs, 1985).

Irrespective of the specific identity of the faecal flora, these results suggest that, even in acid soils, the microbial populations colonizing litter and humus materials are dominated by bacteria, albeit transiently, as a consequence of invertebrate feeding activities.

The effects of gut passage are most pronounced in base-rich soils which are intensively worked by earthworms. The casts contain fewer fungal propagules and denitrifying bacteria, higher counts of total bacteria and more cellulolytic, hemicellulolytic, amylolytic and nitrifying bacteria than unworked soil (Loquet, Bhatnagar & Bouché, 1977). Bhatnagar (1975) estimated that 40% of all aerobic, free-living nitrogen-fixers, 13% of anaerobic nitrogen-fixers and 16% of denitrifying bacteria in the total soil volume were located in a narrow zone a few millimetres around earthworm burrows. Kretzschmar (1978) estimated that this zone constituted only 0.9% of the soil volume in a French pasture but contained 15% of the total soil microflora. Given the magnitude of their casting rates, earthworms must be modifying the dynamics of microbial processes in these soils but this has never been considered explicitly in calculations of microbial generation and turnover times.

Indirect effects of invertebrates on mineral nutrient fluxes

Any animal processes which modify the microbial environment, and hence alter the generation and turnover times of bacteria and fungi, will change the rates of microbial processes. These synergistic interactions have been demonstrated for microfauna (Ingham *et al.*, 1985) and mesofauna (Seastedt, 1984) but are most apparent for the effects of soil- and litter-feeding macrofauna on nitrogen mineralization. For example, the addition of millipedes to leaf litter does not produce a step-wise increment in nitrogen mineralization which might be attributable to excretion by the animals or the lysis of microbial biomass at the onset of feeding (Anderson & Ineson, 1984). Instead, the ammonium and nitrate losses from the material increase gradually over several weeks to levels 2–10 times higher than those found in the absence of animals, and if the animals are removed the enhanced rates of nitrogen mineralization slowly return to control levels. These responses are apparently unrelated to the species of saprotrophic fungi and invertebrates used in the laboratory systems and hence general models can be formulated which quantify the indirect effects of animals on nitrogen mineralization from leaf litter or soil organic matter (Anderson *et al.*, 1985b). Hence, cumulative ammonium-nitrogen mineralization from oak woodland leaf litter in the absence of animals (N_c) is given by the equation

$$N_c = 72.3 (\pm 41.7) + 12.4 (\pm 3.9)T$$

where T is the incubation temperature between 5 and 15 °C.

With litter-feeding animals present in replicate samples the cumulative ammonium-nitrogen mineralization function (N_A) becomes:

$$N_A = 27.8 (\pm 49.7) + 17.1 (\pm 4.6)T + 543 (\pm 133)B + 14.7 (\pm 12.3)BT$$

where B is the 'effective biomass', i.e. the animal biomass (g fresh wt) divided by the dry weight (g) of the resource ($B = 0.1$ to 0.3 in these experiments). The regression coefficients in N_c are not significantly different from the same partial regression coefficients in N_A . Hence the first two functions in N_A are an expression of microbial nitrogen mineralization and the B and BT functions represent the additional effects of animals. The animal-mediated flux is not corrected for excretory nitrogen and is therefore only a partial expression of indirect animal effects. Expressions of N_A for total nitrogen mineralization from litter and humus materials from three oak woodlands are shown in Fig. 3.

These multiple regression functions are not a general expression of nitrogen mineralization by animals and have to be derived empirically for each resource type, but they do show that invertebrates can have significant effects on net nitrogen mineralization, particularly during the early stages of litter decomposition when it is often assumed that net microbial immobilization of nitrogen occurs.

To link the laboratory and field experiments, a series of replicated soil and litter lysimeters was set up in an oak woodland (Anderson *et al.*, 1985a). Treatments were: with or without macrofauna (millipedes, woodlice and earthworms added at the equivalent of 13 g fresh wt m⁻²) and with or without living tree roots (introduced through ports in the sides of the lysimeters). Mineral element concentrations in leachates were monitored for 2 years. Cumulative mineral nitrogen losses from treatments with and without roots, and with and without macrofauna for the first 64 weeks of the experiment are shown in Table 3.

The results show that over the first 32 weeks, from spring to leaf fall, the fauna increased ammonium nitrogen losses by 5.4 kg ha⁻¹ and nitrate nitrogen losses by 6.2 kg ha⁻¹ in the lysimeters without roots; a total of 11.6 kg ha⁻¹ or about a third of the annual nitrogen input in leaf litter. The macrofauna also increased the labile nitrogen pool in the litter and soil organic matter leading to greater mineral nitrogen losses, up to 3.8 kg N ha⁻¹ wk⁻¹, than in the controls, following wetting and drying events during a hot, dry summer (Anderson *et al.*, 1985a). However, after leaf fall in week 33 ammonium nitrogen losses were lower from the lysimeters with animals than those without them until soil temperatures increased the following spring. Roots took up approximately half of the mineral nitrogen flux in all treatments in contrast to undisturbed forest soils where mineral nitrogen was scavenged with high efficiency. None the less, these experiments do show that a small biomass of macrofauna, less than that found in many deciduous forest soils, can have significant effects on seasonal patterns of nitrogen immobilization and mineralization.

Anderson *et al.* (1985b) have predicted that the indirect effects of macrofauna will contribute significantly to nitrogen mineralization where the effective biomass for litter is at least 0.1. Higher values than this are associated with base-rich soils, high-quality litters which decompose rapidly and often a large biomass of earthworms. Under these conditions additional indirect effects on microbial processes are introduced by the burrowing activities of the worms.

Earthworm-worked soils have a higher pore volume, increased

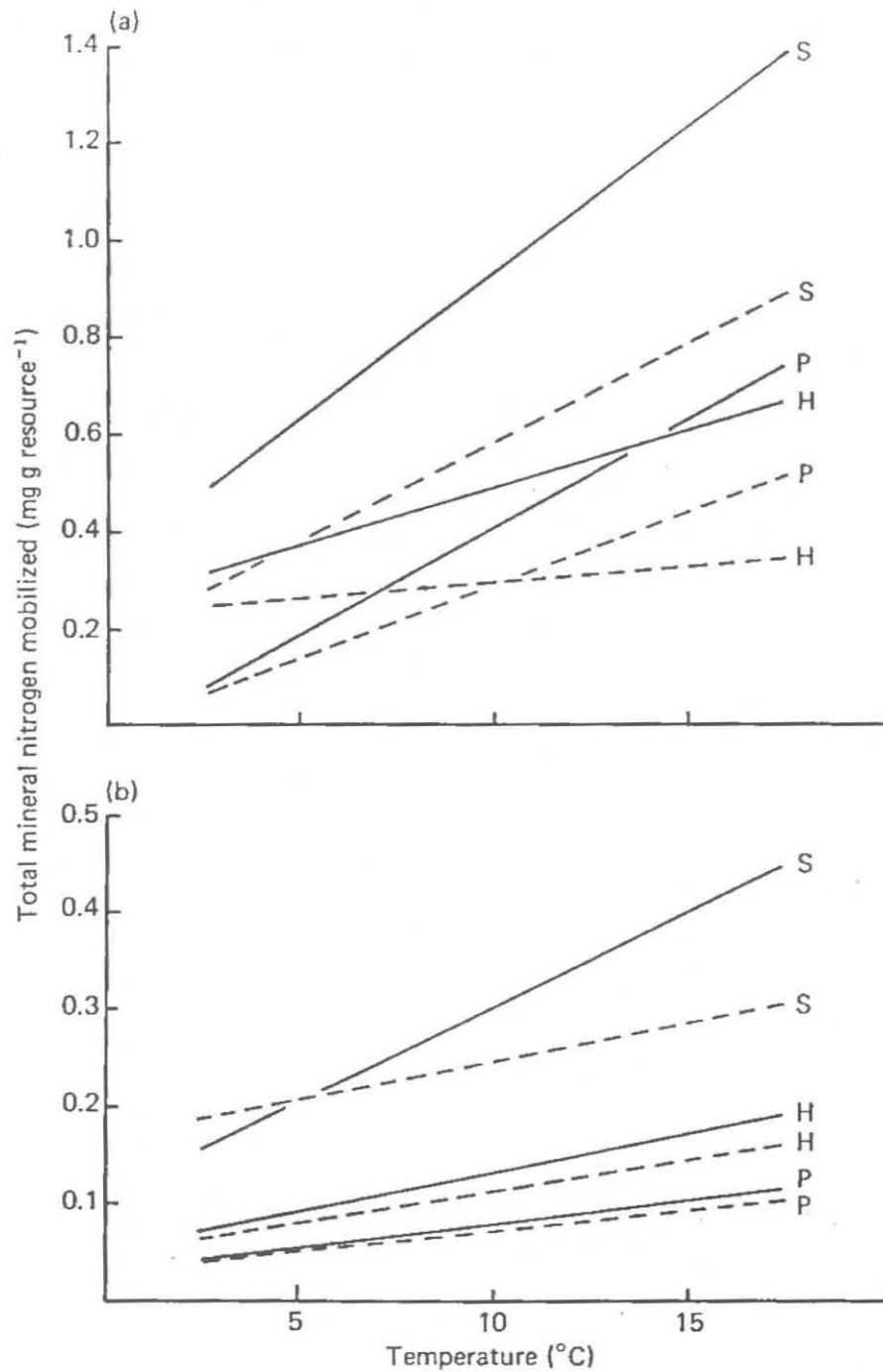


Fig. 3. Expressions of nitrogen mineralization from litter (a) and humus (b) from three oak woodlands (Perridge, P; Hillersdon, H; and Stoke, S) using multiple regression functions based on animal biomass (including zero biomass) and temperature. Nitrogen mineralization with animal effects, at an effective biomass (B) of 0.3, is shown by the solid line, while microbial mineralization (when $B = 0$) is shown by the broken line. The same value of B was used for the litter and humus materials to emphasize the different magnitude of animal effects on the two resource types (note the difference in scale of nitrogen mineralization in a and b). (After Anderson *et al.*, 1985b.)

field water-holding capacity, more water-stable aggregates and higher infiltration rates than soils without earthworms or with surface active species. The introduction of deep-burrowing lumbricid earthworms into New Zealand pastures has dramatically altered soil

Table 3. Cumulative mineral nitrogen losses from a series of small (0.25 m²) lysimeters in an oak woodland over two periods from April to October (weeks 1–32) and November to June (weeks 33–64). Treatments are with and without macrofauna and with and without oak tree root systems. Results are calculated as kg N ha⁻¹ (\pm SE, $n = 3$). For details see text.

Period (weeks)	No roots		Roots	
	Without animals	With animals	Without animals	With animals
Ammonium nitrogen				
1–32	23.26 \pm 1.09	28.68 \pm 0.92	11.27 \pm 3.63	9.89 \pm 1.00
33–64	16.25 \pm 1.13	10.03 \pm 1.47	1.23 \pm 0.37	0.63 \pm 0.02
Nitrate nitrogen				
1–32	8.86 \pm 1.91	15.06 \pm 1.14	2.18 \pm 0.33	2.27 \pm 0.34
33–64	12.20 \pm 0.87	13.46 \pm 1.67	0.79 \pm 0.03	0.46 \pm 0.05

physical conditions and plant rooting depth and has raised pasture productivity by up to 72% (Stockdill, 1982).

RESOLUTION OF MICROSITE PROCESSES

The variable responses of animal–microbial interactions in field and laboratory studies are consistent with the hypothesis that soil organism communities comprise few species with very specific roles in decomposition processes and nutrient cycling. Most functional groups of invertebrates, fungi and bacteria contain a large number of species with broadly overlapping, and often very plastic, trophic capacities.

Swift (1976, 1984) has suggested that fungal communities have a hierarchical structure built up of species groups, or ‘unit communities’ inhabiting individual resource units such as twigs or faecal pellets. The microorganisms in the unit community are assortatively selected from the species pool so that they have the capacity to decompose that resource; interactions between different or adjacent units are minimized. Thus, no matter how much variation there may be in floristic composition between unit communities, it is theoretically only necessary to understand the functioning of a single unit community to establish the principles for decomposition as a whole. The invertebrates are integral components of these unit communities and have very variable associations with different microbial species

assemblages. Anderson (1978) found that the gut contents (higher plant material, bacteria, fungal hyphae and spores) of mites were related to the microhabitats they occupied. Furthermore, the composition of the ingested material showed less variation between different mite species occupying similar microhabitats, defined at a scale of about 0.1 mm, than between the same mite species in different soil and litter horizons.

Different sized organisms will use resources on different scales. Thus microhabitats for assemblages of bacteria, nematodes and protozoans may be defined in a soil aggregate or on a section of fine root, while at the other extreme a single individual of a cord-forming basidiomycete may invade a number of tree boles over an area of more than 100 m² (Thompson & Boddy, 1983).

Evidence from field and laboratory studies shows that the soil is made up of a mosaic of these different-sized patches in different phases of microbial growth; some patches, for example, immobilize nitrogen and others show a new release of nitrogen. Net nitrogen mineralization in bulk soil will only be detectable where microsites releasing nitrogen exceed those immobilizing nitrogen.

The relative importance of animal microbial interactions to these patch dynamics may be predicted from the size-resource relations of organisms in the community. Hence direct contributions to nutrient fluxes may be important where the organisms and resources are of similar size (e.g. amoebae/bacteria; earthworms/leaf litter). On the other hand indirect effects of invertebrates on microbial processes may be more functionally significant where the animal structurally modifies microbial microhabitats and the associated unit community (litter-feeding invertebrates and earthworms ingesting soil).

At an intermediate scale, such as microarthropods grazing on fungal hyphae, the dynamics of the interactions will depend on the animal population densities, the extent of the mycelium, microhabitat structure and the quality of the resource exploited by the fungus.

The micro-, meso- and macrofauna therefore represent different types and scales of perturbation which contribute to these microsite dynamics and hence to mineral element fluxes. While we can identify specific organism interactions in the laboratory, or the synchrony imposed on microbial activities in microsites by passage through the earthworm gut, we are currently unable to link these events to gross soil processes. Plant rooting systems resolve the soil mosaic at a level necessary to optimize nutrient uptake and thus provide

an integrated measurement of the net products of these microsite processes.

As nitrogen availability declines, a greater proportion of new production is allocated below ground (McClaugherty, Aber & Melillo, 1982) and roots become more finely branched to exploit a larger soil volume (Barley, 1970; Fitter, 1985). Under conditions of very low nutrient availability in organic soils, roots become longer lived and, since nutrient uptake is mainly associated with the unsubsized regions of the proliferating tips, their absorptive capacity is reduced. Instead, nutrient uptake is facilitated by the plants reallocating carbon from short-lived root hairs to mycorrhizal associations which have comparatively long-lived and extensive hyphal ramifications through the soil and litter matrix. Microsites with low rates of nitrogen mineralization can thus be exploited efficiently by trees with rooting volumes as low as $0.13\text{--}5.3\text{ cm cm}^{-3}$ compared with 50 cm cm^{-3} for grasses and $5\text{--}25\text{ cm cm}^{-3}$ for intensely cultivated cereals (Bowen, 1984). In low fertility soils both tree roots and the hyphae of vesicular-arbuscular mycorrhizas show increased branching when they encounter local patches of organic matter within the soil matrix (St John, Coleman & Reid, 1983).

On the basis of these rooting patterns it is hypothesized that under conditions of moderate to high nutrient availability the effects of earthworms in promoting a favourable environment for roots are likely to be more important for plant growth than the activities of rhizosphere invertebrates in mediating processes of nitrogen mineralization.

CONCLUSIONS

The understanding of ecosystem and global fluxes of carbon and nitrogen is based on a knowledge of microbial physiological processes operating in microsite environments. Under steady state conditions the products of the microsites are always the net expression of animal-microbial interactions since there are no natural terrestrial environments from which soil invertebrates are excluded. If the system is disturbed then the whole community will undergo adjustment to some new equilibrium state and the reduced or increased activities of the animals will be part of the definition of the new dynamic state of the community. Thus it can be argued that establishing the conditions under which invertebrates make a major contribution

to soil processes may provide greater insight into the responses of soils to major perturbations. At the other extreme, studies on the ecology of specific organisms mediating key nutrient transformations (nitrification, denitrification) or plant processes (root pathogens, nodulating bacteria and mycorrhizas) operate in microsites where animal effects may modify microbial processes expressed in axenic cultures. There is no doubt that animal-microbial interactions are real phenomena in all systems but the quantitative links between species and ecosystem processes cannot be resolved without more synergistic approaches. More integrated studies between soil microbiologists, zoologists, physicists and biochemists are required to assess whether these interactions have manipulative potential or can be regarded merely as a source of variation or 'noise' within extremely heterogeneous soil systems.

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